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Research Article

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National Trade can Drive Range Expansion of Bark- and Wood-Boring Beetles

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Abstract

Several native species of bark- and wood-boring beetles (Coleoptera) have expanded their range within their native biogeographic regions in the last years, but the role of human activity in driving this phenomenon has been underinvestigated. Here we analyze 3 yr of trapping records of native bark- and wood-boring beetles (Cerambycidae and Scolytinae) collected at 12 Italian ports and their surrounding forests to help elucidate the human role in the movement of native species within their native biogeographic region. We trapped several species that occurred either inside or outside their native distributional range within Italy. Species richness and abundance of those species found in the ports located within their native range were most strongly associated with the amount of forest cover in the surrounding landscape, suggesting that they could have arrived in the ports from the nearby forests. The abundance of the species found outside their native range was instead most strongly linked to the amount of national imports arriving at the port where trapping occurred, suggesting that they were likely introduced to the ports from other parts of Italy. This study demonstrates that national sea transportation can favor species range expansion within a country, and confirms that the forests that surround ports can serve as a source of species that can be potentially moved with exports.

Key words: Cerambycidae, human-assisted spread, Scolytinae, trade, wood packaging

The ability of organisms to actively disperse is recognized as one of the main mechanisms driving range expansion of a species both within its native and non-native biogeographic regions (Lester et al. 2007, Arribas et al. 2012). This ability varies strongly among organisms, and usually only those species with high dispersal ability are able to actively invade new territories (Rhainds et al. 2011, Baselga et al. 2012). Nevertheless, rapid national and international trade associated with construction of steamships, canals, highways, and railways offered many organisms the opportunity to exploit these anthropogenic activities and thereby be introduced into new territories and expand their distributional range (Hulme 2009, Hu et al. 2013). Thus, human-assisted dispersal has exacerbated the movement of species among regions and continents (Amano et al. 2016), providing both new opportunities for species with low ability to disperse and more opportunities for those species that already have high dispersal capabilities.

Among the bark- and wood-boring beetles (Coleoptera), many species of Cerambycidae and Scolytinae have both a high dispersal potential (Drag et al. 2011, Chase et al. 2017, Lopez et al. 2017, Meurisse and Pawson 2017) and a strong possibility of hitchhiking in timber and woody materials associated with exported products such as crating and pallets (Haack 2001, 2006; Brockerhoff et al. 2006a; Skarpaas and Økland 2009; Eyre and Haack 2017). Good evidence for this phenomenon can be found when looking at the high numbers of exotic bark- and wood-boring beetles intercepted at ports of entry worldwide (Brockerhoff et al. 2006b, Haack 2006, Rassati et al. 2015a, Wu et al. 2017), recorded as established in new countries (Kirkendall and Faccoli 2010, Rassati et al. 2016, Eyre and Haack 2017) or spreading in non-native habitats (Faccoli et al. 2016, Grilli and Fachinetti 2017, Landi et al. 2017). Moreover, many species of bark- and wood-boring beetles can cause, either directly or indirectly, severe ecological and economic damage in newly invaded ecosystems (Nowak et al. 2001, Aukema et al. 2011, Susaeta et al. 2017). Therefore, these beetles have received great attention in the last few decades, with several studies focused on the mechanisms that drive the invasion process both prior to and after introduction into a new environment (Gilbert et al. 2003, Koch and Smith 2008, Yemshanov et al. 2012), and many of them confirmed active dispersal and human-mediated dispersal as key drivers (Koch et al. 2012, Hu et al. 2013, Gohli et al. 2016). Whether these mechanisms can also drive range expansion of native species within their native biogeographic region is less clear and so far underinvestigated.

In addition to the famous case of range expansion by the mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae) (Robertson et al. 2009), several other examples of bark- and wood-boring beetles expanding their geographic distribution within their native biogeographic region can be found (Rabaglia and Williams 2002, Rabaglia and Valenti 2003, Lightle et al. 2007, Schiefer 2010, Helm and Molano-Flores 2017). Although active dispersal and climate warming have been identified as the main drivers of the range expansion for some bark- and wood-boring beetle species (Čížek et al. 2009, Marini et al. 2012, Raffa et al. 2013), the main means of range expansion within their native biogeographic region is often from ground transportation of firewood, raw logs, and barked wood-products and timber (Baranchikov 1998; LaBonte et al. 2005; Dodds et al. 2010, 2017; Haack et al. 2010; Cranshaw 2011; Jacobi et al. 2012; Ostrauskas and Tamutis 2012). The role of national sea transportation has received less attention mainly because most trapping and early-detection programs carried out at ports focus on exotic species, even though many native species are trapped along with the exotics (Rassati et al. 2015a,b).

Here we analyzed a 3-yr dataset that contained records of native bark- and wood-boring beetles (Cerambycidae and Scolytinae) trapped at several Italian ports, and then compared these collections to other factors in order to better understand which mechanisms influence their communities at each site. First, we determined which species were trapped only in the ports but not in the surrounding forests. Second, we divided those species into two categories based on their known distributional range within Italy: 1) species captured in ports that were located inside their known native distributional range and 2) species captured in ports that were located outside their known native distributional range. And third, we tried to understand the origin of these species by testing two main hypotheses: 1) species that originated from other Italian regions and likely conveyed to the port through national trade, and 2) species that likely originated from nearby forests that surrounded the ports. Although we predicted that the vast majority of these native bark- and wood-boring beetles would come from the surrounding forests, we did expect to find a few species in ports that were located outside their historical native distributional range, which could reflect range expansion through national sea transportation.

Materials and Methods

Trapping Data

We used data from a nationwide trapping program conducted at 12 international Italian ports for three consecutive years (2012–2014) (Table 1), including both published (2012 and 2013 data in Rassati et al. 2015a,b) and unpublished data (2014, D. Rassati). The trapping program was performed using three 12-unit black funnel traps (Econex, Murcia, Spain) at each selected port. In 2012, the same trapping scheme (i.e., three 12-unit black funnel traps per site) was used also in the dominant forest type occurring within a 10-km radius zone around each port. Traps were hung with the collection cup ~1.5 m above ground from suitable supports (e.g., building structures, wire fences, or metal girders at ports, and low tree branches in forests) in relatively open areas, allowing flying insects to approach from all directions. Traps were kept at least 30 m apart in the ports, whereas the distance between the three traps located in the surrounding forests was higher and not constant among sampling sites. This was because the landscape surrounding each port differed, ranging from urban-dominated landscapes where the forested areas were mainly scattered urban parks (e.g., Venezia and Napoli; Table 1), to forest-dominated landscapes where the forested areas were represented by a single or a few large forest patches (e.g., Salerno). Thus the distribution of traps within the forested areas surrounding each port was highly variable (Supp Fig. 1 [online only]). As a general rule, we tried to sample as many of the major forest patches as possible around each port. We initially explored the possibility to deploy more traps in forests surrounding ports, but given that these were checked by port personnel at 2-wk intervals and given our need of keeping the experimental design balanced, we decided for a trapping intensity of three traps per port and three in the nearby forests.

In all years, traps were baited with the same multi-lure blend composed of (-) α-pinene (release rate of 0.77 g/day at 20°C), ethanol (0.3 mg/day at 25°C), ipsenol (+50/-50, 0.4 mg/day at 25°C), ipsdienol (0.16 mg/day at 25°C), and 2-methyl-3-buten-2-ol (10.7 mg/day at 20°C) (Contech Enterprises Inc., Victoria, BC, Canada). The collection cup of each trap was sprayed with a contact insecticide

Table 1. Information on geographical features (name, Italian region, abbreviation, biogeographical unit within Italy, coordinates, and percentage of forest cover within a 10-km radius around each port) and trade data (weighted amount of commodities imported from other Italian regions expressed in tons per year ± SD) for each of the 12 Italian monitored ports

Port	Region of Italy	Port Abbreviation	Biogeographical unit of Italy	Latitude	Longitude	Forest cover (%)	Weighted national trade[a]
Genova	Liguria	Gen	N	44°24′	08°52′	21.08	7,170.26 ± 495.90
Monfalcone	FVG	Mon	N	45°47′	13°32′	25.59	468.59 ± 68.03
Porto Nogaro	FVG	Nog	N	45°47′	13°13′	4.79	136.87 ± 19.87
Ravenna	Emilia Romagna	Rav	N	44°28′	12°15′	9.49	6,265 ± 331.94
Trieste	FVG	Tri	N	45°39′	13°15′	27.45	1,693.20 ± 245.84
Venezia	Veneto	Ven	N	45°27′	12°15′	0.1	5,415.47 ± 399.54
Ancona	Marche	Anc	C	43°37′	13°30′	18.84	860 ± 140.44
Napoli	Campania	Nap	S	40°50′	14°16′	0.63	5,621.98 ± 191.26
Salerno	Campania	Sal	S	40°40′	14°44′	40.76	4,188.34 ± 130.37
Palermo	Sicily	Pal	Si	38°08′	13°21′	6.19	5,253.81 ± 194.67
Cagliari	Sardinia	Cag	Sa	39°15′	09°05′	1.27	6,616.99 ± 400.43
Porto Torres	Sardinia	Tor	Sa	40°53′	08°39′	2.14	1,138.69 ± 68.90

Refer Fig. 1 for graphical representation. FVG, Friuli-Venezia Giulia.

[a]National trade data were obtained as described in the 'Tested variables' subsection.

(Decis, active ingredient Deltamethrin, Bayer Crop Science, Triangle Park, NC, USA) to quickly kill the trapped insects and thereby avoid their escape and consumption by predators (e.g., clerid beetles) that also respond to the attractive blends. The lures were changed based on their expected field-life and cups were resprayed with insecticide at each trap check (i.e., biweekly). Trapped beetles were stored in alcohol and identified morphologically (Balachowsky 1949, Wood and Bright 1992, Bense 1995). Once identified, beetles were classified either as native or exotic to the Italian fauna based on Löbl and Smetana (2010), Kirkendall and Faccoli (2010), and Knížěk (2011). To make the datasets from all ports more comparable, we considered only those collection records that occurred when the trapping program was active at all ports and in all years (late June through early September).

Assigning Beetles to a Specific Italian Geographic Range

For the native Italian bark- and wood-boring beetles collected, we first split the records into two main categories: 1) species that were trapped both in ports and in the surrounding forests; and 2) species that were trapped in ports but not in the surrounding forests. The second group was then further divided into two categories that represented the focus of this study: 1) native species trapped at ports located within their native distributional range in Italy ('inside' species), and 2) species trapped at ports located outside of their native distributional range in Italy ('outside' species).

For bark and ambrosia beetles (Scolytinae), information on the national distribution of each species was obtained from the revised checklist of the Italian Curculionoidea (Colonnelli 2003), which is the most recent checklist available in Italy. In this publication, collection records are reported for five biogeographic subunits: northern Italy (N), central Italy (C), southern Italy (S), Sicily (Si), and Sardinia (Sa) (Fig. 1). The national checklist by Colonnelli (2003) was then updated with new published records (Supp Table 1 [online only]). For the longhorned beetles (Cerambycidae), information on their Italian distribution was obtained from the Italian checklist by Sama and Rapuzzi (2011), which provided collection records for each of the 20 recognized regions in Italy (Supp Fig. 1 [online only]). Therefore, to make the two checklists more comparable, we pooled the regional cerambycid records to match the five biogeographical regions used for the scolytines (Supp Table 1 [online only]). Although we cannot exclude that there were differences in the scolytine and cerambycid trapping efforts throughout Italy, the two above-mentioned publications were based on all the principal insect collections existing in Italy. Thus, for the present publication, we considered these two lists to be correct and exhaustive.

Tested Variables

We tested two variables that could influence the diversity of the bark- and wood-boring beetle species trapped at the Italian ports. The first variable related to Italian national trade data, expressed as the amount in tons of all commodities, excluding liquids, imported from all other regions of Italy outside the region where the port is located (Table 1). This information was obtained from the Italian National Institute of Statistic's database for the years 2012–2014 (ISTAT 2017). The values provided in this database are, however, aggregated per region and to our knowledge no information at a finer resolution (port scale) is available. It is clear that the aggregated value of the regional imports coincides with the value of imports for individual ports when there is only one port in a region (e.g., Ravenna for the Emilia Romagna region or Ancona for the Marche

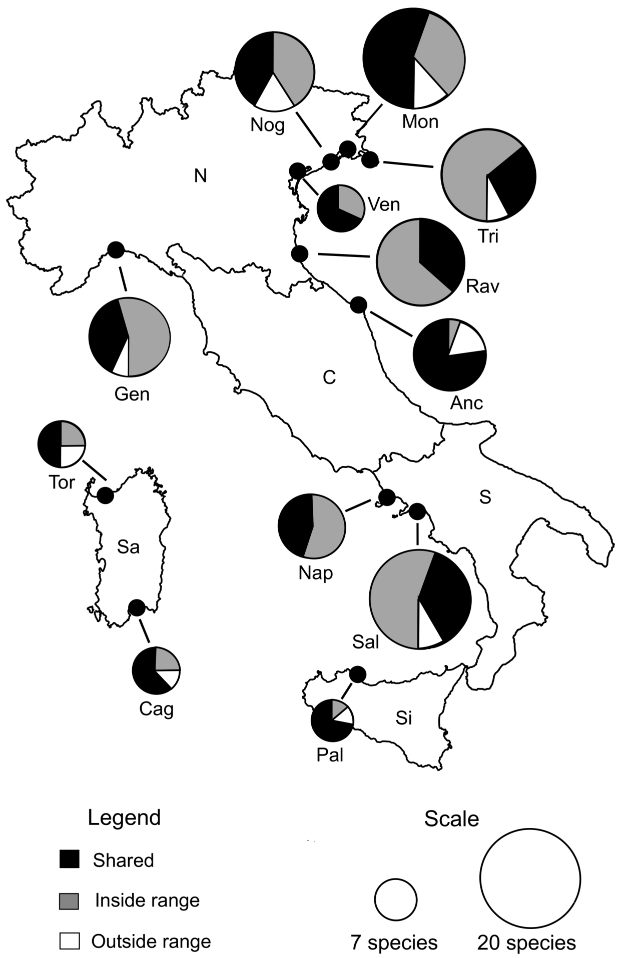

Fig. 1. Map of Italy describing the community of scolytines and cerambycids trapped at several ports of entry during 2012–2014. Circle size indicates the number of trapped species. The various colors within each circle indicate different categories of the trapped beetle species: black = percentage of species shared between ports and their surrounding forests; grey = percentage of species trapped at the ports but not in the nearby forests that were located in regions within their native distributional range ('inside' species); and white = percentage of species trapped at the ports but not in the nearby forests that were located in regions outside their native distributional range ('outside' species). Ports are indicated with black dots. Port abbreviations are given in Table 1. N: northern Italy; C: central Italy; S: southern Italy; Si: Sicily; and Sa: Sardinia.

region; Supp Fig. 1 [online only). However, this is not the case when there are two or more large ports in the same region (e.g., Napoli and Salerno in the Campania region; Supp Fig. 1 [online only]). In these latter cases, we used the values of international trades, which are available for individual ports, as a proxy to weight the national trade of the ports within the same regions. In particular, we first calculated the mean amount of imported commodities per year (2012–2014) for all ports (both those where the trapping occurred and those where it did not) present in the same region (Supp Fig. 1 [online only] and Supp Table 2 [online only]). Then we calculated the percentage of imports for each port within a region and used those percentages to weight the regional trade data for each individual port (Supp Table 2 [online only]). Data on international trades were obtained from the national association of the Italian port's database (Assoporti 2017) or directly from the port authority (Porto Torres). We did not include in our analysis the international trade data from other countries where the Italian native beetles are also present because no import data were available for individual Italian ports by country of origin.

The second tested variable was the amount of forest cover (%) occurring within a 10-km radius surrounding each port (Table 1). This variable was calculated in ArcGIS 10.0 based on digital aerial photographs (Google Earth). For more detail, polygons representing the forest areas were digitized directly in Google Earth excluding single trees, hedgerows, or green areas with an area smaller than 100 m^2. Then, in ArcGIS, the centroid of each port was determined along with a 10-km-wide zone around it. Finally, the percentage of landscape covered by forest within each 10-km-wide zone was calculated for each port, after having excluded the sea area. Although we tested the influence of forest cover on the community of species trapped at ports in an earlier study (Rassati et al. 2015a), it was important to include this variable again in the present study to better understand the relative importance of national trade and forest cover in shaping the beetle communities found at ports of entry. We also explored the possibility to test the effect of the distance from the port to the nearest forest patch on the beetle community trapped at the ports, but this variable was highly correlated with the amount of forest cover (i.e., ports surrounded by a low amount of forest cover and dominated by urban areas were those that tended to be more distant from the nearest forest patch). Thus, in our analyses, we considered only the amount of forest cover.

Statistical Analyses

Different statistical approaches were used to analyze the 'inside' and 'outside' categories of beetle species considered in this study. For 'inside' species collected exclusively at ports located inside their native distributional range within Italy, the influence of national trade and forest cover on species richness and abundance was tested using a generalized linear mixed model. The mean number of species (i.e., species richness) and number of individuals collected (i.e., abundance) of all species combined per year at each port was the response variable. Abundance was log-transformed to improve linearity. The model included the port as a random factor and was fitted using the 'lme' function in the package nlme (Pinheiro et al. 2017) for R version 3.2.0 (R Development Core Team 2015).

For 'outside' species collected at ports located outside their native distributional range within Italy, we used a different statistical approach because the number of species included in this category was relatively low. Thus, we considered only the abundance of each 'outside' species. We used a linear regression ('lm' function for R) approach, where the abundance of each trapped 'outside' species was the response variable and the explanatory variables were 1) the weighted amount of commodities imported from regions of Italy where the 'outside' species was reported to be native and 2) the corresponding percentage of forest cover present in the landscape surrounding each port. An alpha level of 0.05 was used to test for significance in all analyses.

Results

General Results

Overall, 52 species of bark- and wood-boring beetles (7,702 individuals) were trapped in the ports (2012–2014) and nearby forests (2012 only), including 39 species of scolytines (7,518 individuals), and 13 species of cerambycids (184 individuals) (Supp Table 1 [online only]). Among the scolytines, true bark beetles were more diverse and abundant (34 species, 7,174 individuals) than ambrosia beetles (five species, 341 individuals) (Supp Table 1 [online only]).

Orthotomicus erosus (Wollaston) (Coleoptera: Curculionidae) was the most abundant scolytine species collected (3,948 individuals; 52.5% of total), followed by *Hylurgus micklitzi* Wachtl (1,607; 21.3%) and *Ips sexdentatus* (Borner) (1,037; 13.7%). Among the cerambycids, *Spondylis buprestoides* (L.) (64; 34.7%) and *Acanthocinus griseus* (F.) (44; 23.9%) were the two most abundant species collected. In contrast, only a single individual was trapped for several species of scolytines and one cerambycid species (Supp Table 1 [online only]).

The ports of Monfalcone and Trieste had the highest species richness (20 spp; Fig. 1), whereas the highest number of individuals (i.e., abundance for all years combined) was found in Ancona (2,148), followed by Ravenna and Salerno (1,602 and 1,317, respectively; Supp Table 1 [online only]). In contrast, Palermo and Porto Torres were the ports with the lowest number of species (7 spp; Fig. 1) and individuals (8 and 55, respectively) (Supp Table 1 [online only]).

When analyzing the communities of species found at each port, we found that the ports of Ancona and Palermo registered the highest proportion of species shared between the port and its surrounding forests (71%), followed by Genova and Napoli (41%) (Fig. 1). Ravenna was the port with the highest proportion of 'inside' species trapped only within the port (0.61%), whereas Ancona was the port with the highest proportion of 'outside' species that were exclusive to the port (0.21%) (Fig. 1).

Species Trapped at Ports Within Their Native Range

Overall, 39 species of scolytines and cerambycids, corresponding to 273 individuals, were trapped at ports located inside their native distributional range within Italy (Table 2). Of these, 28 were scolytines and 11 were cerambycids. *Ips typographus* (L.) and *Hylurgus ligniperda* (F.) were the most abundant scolytines (48 and 35 individuals; 21.8 and 15.9% of total, respectively), whereas *Hylotrupes bajulus* (L.) (13; 24.5%) and *Monochamus galloprovincialis* (Olivier) (12; 22.6%) were the two most abundant cerambycids (Table 2). The port of Trieste had the highest numbers of 'inside' species and individuals (12 and 135, respectively), whereas only one 'inside' species was found in Palermo and Ancona (Fig. 1, Table 2). Most of the 38 'inside' species collected are known to develop in conifers (20), whereas, among the others, 13 develop in broadleaf trees, three in both conifers and broadleaf trees, and one in herbaceous plants (Table 2). Both species richness and abundance of the 'inside' species were positively associated with the amount of forest cover occurring in the landscape surrounding the ports ($t = 2.93$; df = 1,9; $P = 0.016$ and $t = 2.82$; df = 1,9; $P = 0.027$, respectively), but not by the amount of national imports ($t = 0.92$; df = 1,9; $P = 0.38$ for species richness and $t = 1.19$; df = 1,9; $P = 0.26$ for abundance). In general, the higher the percentage of forest cover, the higher was the mean number of species and individuals trapped per year at the individual ports (Fig. 2).

Species Trapped at Ports Outside Their Native Range

A total of 11 species, represented by 29 individuals, were trapped at ports located outside their native geographical range within Italy (Table 2 and Supp Table 3 [online only]). Ten of these species were scolytines, whereas only one was a cerambycid (*Arhopalus rusticus* L.). *Pityokteines vorontzowi* (Jakobson) was the most abundant 'outside' species collected (five individuals; 17.2% of total), followed by *Pityogenes calcaratus* (Eichhoff), *Carphoborus perrisi* (Chapuis),

Table 2. List of Scolytinae and Cerambycidae species trapped exclusively in the ports and not in the surrounding forests, divided into those species that were trapped within their native range in Italy ('inside' species) and species trapped outside their native range in Italy ('outside' species)

Beetle species	Historical distributional range within Italy	Abundance (No. collected)	Ports of interception	Years of interception within ports	Larval host
'Inside' species					
Scolytinae					
Anisandrus dispar (F.)	N, C, S, Si, Sa	1	Sal	2013	Broadleaf
Carphoborus perrisi (Chapuis)	S, Si, Sa	12	Pal, Sal	2012–2014	Broadleaf
Crypturgus cinereus (Herbst)	N, S	5	Gen, Mon, Nap, Rav	2012–2014	Conifer
Crypturgus cribrellus Reitter	N, S	3	Nap, Nog, Rav	2013, 2014	Conifer
Crypturgus mediterraneus Eichhoff	N, S, Sa	5	Nap, Sal	2013	Conifer
Crypturgus numidicus Ferrari	C, S, Si, Sa	3	Nap	2012, 2013	Conifer
Crypturgus pusillus (Gyllenhal)	N, C, S	8	Gen, Nap	2013	Conifer
Hylesinus oleiperda F.	N, C, S, Si, Sa	2	Rav, Tri	2012, 2014	Broadleaf
Hylurgus ligniperda (F.)	N, C, S, Si, Sa	35	Nog, Tri	2012–2014	Conifer
Hylurgus micklitzii Wachtl	N, C, S, Si, Sa	10	Mon, Rav, Tri	2012–2014	Conifer
Hypoborus ficus Erichson	N, C, S, Si, Sa	1	Tri	2012	Broadleaf
Ips acuminatus (Gyllenhal)	N, S, Si	10	Mon, Nog, Rav	2013, 2014	Conifer
Ips amitinus (Eichhoff)	N, C	2	Mon, Tri	2012, 2013	Conifer
Ips sexdentatus (Börner)	N, C, S, Si, Sa	18	Sal	2013, 2014	Conifer
Ips typographus (L.)	N, C, S, Sa	48	Gen, Rav, Tri	2012, 2013	Conifer
Liparthrum mori (Aubé)	N, S, Sa	2	Gen, Sal	2012, 2013	Broadleaf
Orthotomicus laricis (F.)	N, C, S, Sa	6	Nog, Tri, Ven	2012–2014	Conifer
Orthtomicus proximus (Eichhoff)	N, C, S	3	Nog	2012	Conifer
Phloeotribus cristatus (Fauvel)	N, C, S, Si, Sa	1	Sal	2013	Broadleaf
Pityogenes chalcographus (L.)	N, C	3	Gen, Mon, Nog	2013	Conifer
Pityokteines curvidens (Germar)	N, C, S	1	Mon	2012	Conifer
Scolytus kirschii Reitter	N, C, S	1	Tri	2014	Broadleaf
Scolytus multistriatus (Marsham)	N, C, S, Si, Sa	24	Rav, Sal, Tri	2012–2014	Broadleaf
Scolytus rugulosus (Müller)	N, C, S, Si, Sa	1	Sal	2013	Broadleaf
Trypodendron lineatum (Olivier)	N, C, S, Sa	9	Tri, Ven	2012, 2013	Conifer
Trypophloeus asperatus (Gyllenhal)	N	1	Rav	2013	Broadleaf
Xylocleptes bispinus (Duftschmid)	N, C, S, Si, Sa	2	Nap, Tri	2012, 2014	Broadleaf
Xyleborus eurygraphus (F.)	N, S, Si	3	Sal	2013, 2014	Conifer
Cerambycidae					
Aromia moschata (L.)	N, C, S	3	Rav, Sal	2013, 2014	Broadleaf
Chlorophorus varius (Müller)	N, C, S, Sa, Si	10	Mon, Nog	2012, 2013	Broadleaf
Gracilia minuta (F.)	N, C, S, Sa, Si	1	Cag	2012	Broadleaf
Hylotrupes bajulus (L.)	N, C, S, Sa, Si	13	Gen, Nap, Rav, Sal	2012–2014	Conifer
Monochamus galloprovincialis (Olivier)	N, C, S, Si	12	Gen	2013, 2014	Conifer
Niphona picticornis Mulsant	N, C, S, Si, Sa	1	Cag	2014	Broadleaf/Conifer
Parmena solieri Mulsant	N, Sa	3	Tor	2013	Herbaceous plant
Penichroa fasciata (Stephens)	N, C, S, Sa, Si	3	Tor	2013	Broadleaf/Conifer
Spondylis buprestoides (L.)	N, C, S, Si	3	Anc, Gen	2013	Conifer
Stictoleptura cordigera (Fuessly)	N, C, S, Si, Sa	3	Rav, Tri, Ven	2013, 2014	Broadleaf
Trichoferus fasciculatus (Faldermann)	N, C, S, Sa, Si	1	Gen	2013	Broadleaf/Conifer
'Outside' species					
Scolytinae					
Carphoborus perrisi (Chapuis)	S, Si, Sa	4	Mon, Tri	2012, 2013	Broadleaf
Cryphalus piceae (Ratzeburg)	N, S	4	Pal	2013	Conifer
Crypturgus cinereus (Herbst)	N, S	1	Anc	2014	Conifer
Crypturgus mediterraneus Eichhoff	N, S, Sa	2	Anc	2013	Conifer
Crypturgus numidicus Ferrari	C, S, Si, Sa	1	Nog	2014	Conifer
Orthotomicus proximus (Eichhoff)	N, C, S	3	Cag	2014	Conifer
Pityokteines vorontzowi (Jakobson)	S, C	5	Mon, Nog	2012, 2013	Conifer
Pityogenes calcaratus (Eichhoff)	S, Sa	4	Gen	2014	Conifer
Pseudothamnurgus mediterraneus (Eggers)	C, S	3	Tor	2014	Broadleaf
Xylocleptes biuncus Reitter	N, C	1	Sal	2013	Broadleaf
Cerambycidae					
Arhopalus rusticus (L.)	N, S, Si	1	Anc	2014	Conifer

Reported for each species is its historic distributional range within Italy (according to Colonnelli (2003) for scolytines, and Sama and Rapuzzi (2011) for cerambycids), abundance (number of trapped individuals in all years), the ports and years where/when they were trapped, and the main larval host plant category. Port abbreviations are given in Table 1.

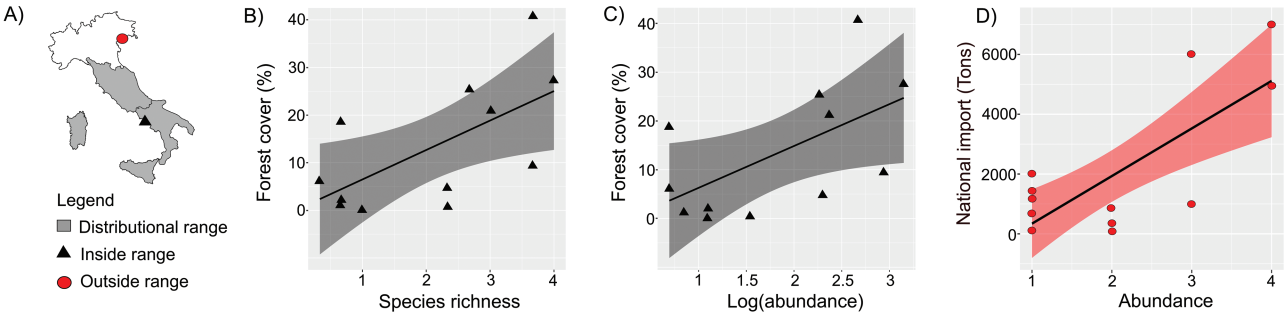

Fig. 2. Plots showing the effect of the significant variables on the two groups of species considered in this study. (A) Example of a hypothetical species trapped inside (triangle) or outside (circle) its native distributional range within Italy. The mean number of 'inside' species (B) or individuals (C) trapped per year at each monitored port are shown in relation to percent forest cover in an area within 10 km of the port. (D) The number of individuals for each 'outside' species trapped in a given year and at a given port are shown in relation to the amount of national imports (tons) arriving in that given year and at that given port. Panels were drawn using the 'ggplot' function from the library 'ggplot2' in R.

and *Cryphalus piceae* (Ratzeburg) (four individuals each). In addition, *Pityokteines vorontzowi* and *Carphoborus perrisi* were the only two 'outside' species to be collected at more than one port (Monfalcone and Trieste and Monfalcone and Nogaro, respectively) and in more than 1 yr (Supp Table 1 [online only]). Ancona (Central region) was the port with the highest number of outside species (3), whereas Porto Nogaro, Genova, and Monfalcone (Northern region) were the ports with the highest number of collected 'outside' individuals (4) (Fig. 1, Table 2). Most of the trapped 'outside' bark- and wood-boring beetle species develop in conifers (8 of 11 species), whereas three species typically develop in broadleaf trees (Table 2 and Supp Table 3 [online only]). With regards to the tested variables, we found that the abundance of trapped 'outside' species was positively associated with the amount of imported commodities (t = 4.17; df = 1,12; P = 0.001; Fig. 2), but not by the percentage of forest cover occurring in the landscape surrounding the ports (t = -1.48; df = 1,12; P = 0.16).

Discussion

Several species of bark- and wood-boring beetles have increased their geographic range in recent decades, not only becoming established in new continents (Rassati et al. 2016, Eyre and Haack 2017), but also within countries in their native biogeographic regions (Rabaglia and Williams 2002, Rabaglia and Valenti 2003, Lightle et al. 2007, Helm and Molano-Flores 2017). Besides active dispersal and climate warming (Cizek et al. 2009, Marini et al. 2012, Raffa et al. 2013), human activities, such as log and firewood movement, are also known to play a role in this phenomenon of within-country range expansion (Baranchikov 1998, Dodds et al. 2010, Cranshaw 2011, Jacobi et al. 2012). Through the analysis of the community of native scolytines and cerambycids trapped at Italian ports, our study elucidated another mechanism by which native species can be moved within the same country as well as potentially to other countries. Our findings suggest first that forests near ports can serve as a source of native species that can be moved in wood packaging associated with exports, and second, that national sea transportation can promote range expansion of species within countries where they are native. Such findings underscore the importance of identifying and recording not only exotic species trapped or intercepted at ports of entry but also native species.

We found that the communities of native bark- and wood-boring beetles trapped at ports were composed of a wide variety of species, some of which were trapped exclusively inside the ports and not in the surrounding forests. In addition, most native species that were trapped at ports were captured within the species' native range ('inside' species), suggesting that they could have arrived from nearby forests. In fact, species richness and abundance of the 'inside' species was positively associated with the amount of forest cover surrounding the ports, even though these species were not trapped in the nearby forests. However, when discussing these trends, it is important to consider some of the limitations of our data. First, sampling in the nearby forests was only carried out in 2012. Although we assumed that the community of bark- and wood-boring beetles found in 2012 was representative of the communities that were present in 2013 and 2014, it is probable that more species would have been discovered if we had sampled the forests in multiple years. Second, only the dominant forest type was sampled around each port in 2012, and thus we cannot state the diversity of beetles trapped in the sampled forests was fully representative of the beetle community present near each port. And third, although the trapping protocol we used was developed specifically for trapping many species of beetles at ports of entry and their surrounding forests (Rassati et al. 2014), we cannot state whether our trapping intensity and lure selection was sufficient to sample the entire community of bark- and wood-boring beetles present. Nevertheless, our results suggest that native species can move from inland forests to local ports (Rassati et al. 2015a), where they can potentially colonize woody materials used to secure commodities scheduled for export while the latter reside at the port area before being shipped. Previous studies, in fact, demonstrated that both scolytines and cerambycids can colonize wood-packaging materials after phytosanitary treatments (e.g., heat or fumigation, IPPC 2016), especially if residual bark is present (Evans 2007, Haack and Petrice 2009). Therefore, a careful analysis of species living in the forest areas surrounding ports can help predict which species are likely to be conveyed within wood packaging materials associated with exports.

We also found that some of the species trapped exclusively in the ports were found outside their native geographic range ('outside' species), and their abundance was positively associated with the amount of national imports arriving at each port. Although the movement of bark- and wood-boring beetles through international trade is a well-known mechanism to explain the exchange of species among continents (Haack 2001, 2006; Brockerhoff et al. 2006a; Skarpaas and Økland 2009; Wu et al. 2017), the role of national trade in moving native species within their native biogeographic region has largely been underinvestigated. In Italy, nearly any product can be moved among the many ports in any given year (ISTAT 2017), and given that many commodities are associated with wood packaging materials (Haack 2006, Brockerhoff et al. 2006b, Rassati et al. 2015a, Wu et al. 2017), there is a chance that they could also transport bark- and wood-boring beetles. Within Italy, as well as most of the European Union (EU), wood packaging that is shipped domestically does not have to be treated similarly to wood used for international exports, although exceptions exist (e.g., woody materials imported from Portugal or other areas where there are infestations of quarantine pests) (EUR-Lex 2017). This EU policy is similar to that used in many other parts of the world in which domestic wood packaging is not required to be treated to ISPM 15 specifications, such as in the USA (USDA APHIS 2011). Given the above, it is clear that domestic wood packaging could transport native bark- and wood-boring beetles through internal trade, providing the opportunity to expand their within-country range, and thereby overcome geographic and climatic barriers or any type of low inherent capacity to actively disperse (Krascsenitsová et al. 2013, Gohli et al. 2017). It is important to underscore that the lack of data on imports from the other countries where the bark- and wood-boring beetles considered in this study are also found did not allow us to exclude the possibility that some of the 'outside' species were actually introduced on imports from countries outside of Italy. Nevertheless, the previously known distributional range and the main ecological and biological characteristics of the 'outside' species suggest that it is unlikely that they were already present in the forests surrounding the ports in which they were collected. Some of these species, for example, have a typical Mediterranean distribution but were found in northern regions where their hosts do not occur and where the climate is very different than what they experience in their native range (e.g., *Pseudothamnurgus mediterraneus* (Eggers), *Crypturgus numidicus* Ferrari, *Crypturgus mediterraneus* Eichhoff, *Carphoborus perrisi* (Chapuis), *Ptyokteines vorontzowi* (Jakobson), and *Pityogenes calcaratus* (Eichhoff)). Others, instead, have a typical continental distribution covering both northern and southern Italy (e.g., *Orthotomicus proximus* (Eichhoff), *Cyphalus piceae* (Ratzeburg), and *Crypturgus cinereus* (Herbst)) but they were recorded as 'outside' species in the major Italian islands, which are geographically isolated from the continent and where the climate is typically Mediterranean.

In general, we found that the communities of bark- and wood-boring beetles trapped at ports located inside a species native range ('inside' species) included both scolytines and cerambycids, whereas all but one 'outside' species were scolytines. The first trend can be partly explained by the fact that both groups of beetles are able to fly the typical short distances between ports and their surrounding forests, even though the active flight ability of cerambycids (Drag et al. 2011, Lopez et al. 2017) is generally higher than that of scolytines (Kees et al. 2017, Seo et al. 2017). To explain the second trend, instead, it is important to consider that, given the smaller size and the shorter generation time of scolytines, the number of individuals potentially emerging from a given piece of wood packaging is higher for scolytines than for cerambycids (Haack and Slansky 1987; Haack 2006, 2017, Rassati et al. 2016). It is also worth noting that the vast majority of species found both inside and outside their native distributional range were species that develop primarily in conifers. This trend can be attributed to both the typical type of timber used to construct wood packaging in Italy, which is usually conifers (Casolla 2009), and to the higher attractiveness of the lures we used to bait the traps towards conifer-associated beetles (Rassati et al. 2015a, Millar and Hanks 2017).

Worldwide, several monitoring programs for bark- and wood-boring insects have been carried out (Brockerhoff et al. 2006b, Bashford 2008, Rabaglia et al. 2008, Rassati et al. 2015a,b) but none of them have investigated which factors shaped the communities of the native species that were trapped along with the exotic species. In the present study, we demonstrated the importance of identifying and analyzing the pool of native species that can be trapped at ports, both from an ecological point of view, documenting range expansion of native species, and from a practical point of view, allowing lists to be created of the most likely borers to be moved in trade. Future studies could compare the kinds of native species found at national ports with lists of insects that other countries have intercepted on imports from that particular country. Such comparisons would allow exploring whether native species found inside ports and their surrounding forests can be used to predict the pool of potential invaders to other countries. For example, considering the number of distinct interceptions of wood borers (identified to at least the genus level) on exports from Italy that were made in the United States during 1985–2000 (Haack 2006, Supp Table 1 [online only]), the most commonly intercepted cerambycids and scolytines were species of *Monochamus* and *Ips*, respectively. These rankings from Haack (2006) are very similar to what we collected inside the ports in the present study where *Monochamus* individuals were the second most commonly collected cerambycids and *Ips* individuals were the most commonly collected scolytines (Table 2). Such information could help improve targeting of potential invaders in early-detection trapping programs carried out around the world.

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Author contributions

D.R. conceived the study, analyzed the data, and wrote the first draft of the manuscript. D.R. and M.F. identified the beetles. M.F., M.K., and R.A.H. contributed to, edited and approved the final manuscript.

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